# Browsing lawns? Responses of Acacia nigrescens to ungulate browsing in an African savanna

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# BROWSING LAWNS? RESPONSES OF *ACACIA NIGRESCENS* TO UNGULATE BROWSING IN AN AFRICAN SAVANNA

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*Abstract*. We measured browsing-induced responses of *Acacia* trees to investigate "browsing lawns" as an analogy to grazing lawns in a semiarid eutrophic African savanna. During the two-year field study, we measured plant tolerance, resistance, and phenological traits, while comparing variation in leaf nitrogen and specific leaf area (SLA) across stands of *Acacia nigrescens,* Miller, that had experienced markedly different histories of attack from large herbivores. Trees in heavily browsed stands developed (1) tolerance traits such as high regrowth abilities in shoots and leaves, high annual branch growth rates, extensive tree branching and evidence of internal N translocation, and (2) resistance traits such as close thorn spacing. However, phenological "escape" responses were weak even in heavily browsed stands. Overall, browsing strongly affected plant morpho-functional traits and decreased both the number of trees carrying pods and the number of pods per tree in heavily browsed stands. Hence, there is experimental evidence that tolerance and resistance traits may occur simultaneously at heavily browsed sites, but this comes at the expense of reproductive success. Such tolerance and resistance traits may coexist if browsers trigger and maintain a positive feedback loop in which trees are continually investing in regrowth (tolerance), and if the plant's physical defenses (resistance) are not nutritionally costly and are long-lived. Our results confirm that chronic browsing by ungulates can maintain *A. nigrescens* trees in a hedged state that is analogous to a grazing lawn. Further research is needed to fully understand the long-term effects of chronic browsing on reproduction within such tree populations, as well as the overall effects on nutrient cycling at the ecosystem level.

*Key words:* Acacia nigrescens; *compensatory growth; grazing lawns; herbivory; Kruger National Park, South Africa; plant defensive traits; resistance; savanna; spinescence; tolerance.*

## Introduction

Plant responses to herbivore attack can involve chemical and mechanical defenses, as well as growth responses (e.g., mass compensation or changes in plant phenology) that reduce the impact of herbivory (Paige 1992, Houle and Simard 1996, Lennartsson et al. 1997, Agrawal 1998, 2000, Oba et al. 2000). Herbivore-induced defenses may be categorized (see Agrawal 2000) into (1) plant resistance traits that reduce herbivore performance or damage, (2) tolerance traits (i.e., regrowth such as mass compensatory growth abilities) that reduce negative effects when herbivore damage has already occurred, and (3) phenological "escape" that reduces plant availability when herbivores are most active.

Recently, attention has been paid to the interplay of such defensive traits and their consequences for plant ecological and/or evolutionary traits (Rosenthal and Kotanen 1994, Strauss and Agrawal 1999, Stowe et al. 2000, Stinchcombe and Rausher 2002). For instance, increased regrowth abilities of both grass and herb species have been observed after chronic damage by grazers (McNaughton 1983, Paige and Whitham 1987, Nilsson et al. 1996), and the "grazing lawn" phenomenon (McNaughton 1984) is now well understood. That is, ungulate grazers are able to maintain permanent "grazing lawns" through a positive feedback loop (grazing–regrowth–regrazing) that generates enhanced productivity from a short sward. Further empirical studies have shown positive relationships between regrowth ability and reproductive success (Lennartsson et al. 1997, Agrawal 1998, Freeman et al. 2003), while tolerance and resistance traits have been observed in woody plant species exposed to ungulate browsing in various ecosystems, from tropical savannas to boreal forests (Cooper and Owen-Smith 1986, Bergström and Danell 1987, du Toit et al. 1990, Edenius et al. 1993, Dangerfield and Modukanele 1996, Gadd et al. 2001). However, despite the extensive literature on plant defensive mechanisms, the potential trade-offs associated with varying tolerance or resistance traits in wild plants remain controversial (Leimu and Koricheva 2006). Plant responses to herbivory are expected to depend on resource availability (Bryant et al. 1983, Coley et al. 1985, Herms and Mattson 1992), interspecific competition, and/or frequency and intensity of disturbance events. Accordingly, a trade-off

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between different defensive strategies may occur, depending on the interactive effects of different key environmental factors on plant growth (Rosenthal and Kotanen 1994).

The question still remains whether different plant defensive traits (tolerance, resistance, and phenological "escape") may occur simultaneously but in varying degrees of expression across woody plants with different histories of attack from herbivores. We also question whether tolerance and resistance traits are associated with short-term or long-term reproductive success. If short-term, this might confer an advantage to some damaged plants over less damaged plants with low defensive traits (Belsky et al. 1993, Strauss and Agrawal 1999). If long-term, this could be expressed as enhanced survival of heavily browsed plants that achieve reproduction during ephemeral "windows" of low browsing pressure. Such questions are central to assessing the validity of the analogy that has been drawn between grazing lawns and the densely hedged canopies of trees that sustain heavy browsing pressure (McNaughton 1984, du Toit et al. 1990).

We studied six monospecific stands of a palatable woody species, *Acacia nigrescens* Miller, that have experienced markedly different browsing intensities for decades, and presumably centuries, in the central region of the Kruger National Park, South Africa (see du Toit 2003, Naiman et al. 2003). Firstly, we measured plant traits known to provide tolerance to damage (see Stowe et al. 2000) such as regrowth ability (e.g., shoot and leaf biomass, shoot and branch growth rates) and plant architecture (e.g., tree branching, shoot meristem availability). We tested whether such tolerance traits differed between heavily and lightly browsed *Acacia* stands with and without artificial clipping. The outcomes are crucial for supporting or rejecting the sustainability of the feedback loop (browsing–regrowth–rebrowsing) proposed by du Toit et al. (1990) for the same *Acacia*-dominated plant community in central Kruger.

Secondly, we investigated whether thorn size and spacing on external branches of *A. nigrescens* trees (i.e., resistance traits) were different between heavily and lightly browsed trees. As with many other *Acacia* species, *A. nigrescens* has physical defenses (recurved thorns and prickles) that reduce the intake rates of browsers, as has been shown in other palatable woody species (Cooper and Owen-Smith 1986, Milewski et al. 1991, Gowda 1996). Spinescence is a distinctive feature of many woody species in semiarid southern African savannas (Huntley 1982), and especially of fine-leaved savannas on relatively nutrient-rich geological substrates (Scholes et al. 2003). Finally, we tested whether changes in plant phenological traits, such as the occurrence and length of the main period of annual growth, as well as seed production, varied across a strong browsing gradient over two consecutive years.

## Study Sites and Methods

### *Study system*

Our study was based at the Tshokwane ranger station (24°47′ S, 31°52′ E) in the central region of the Kruger National Park, South Africa. Field experiments were carried out during 2002–2003 in the Satara land system, which mainly consists of fine-leaved tree savanna or bushveld, dominated by *Acacia nigrescens*, *Sclerocarya birrea*, and *Dichrostachys cinerea* (Venter et al. 2003). The geologic substrate is predominantly basaltic, and the rainfall averages 570 mm per annum, with 80% of the precipitation concentrated in the wet season from October to March. However, rainfall from September 2002 to November 2003 was particularly low: ~200 mm in total. A relatively intense year-round browsing regime is imposed by giraffes (*Giraffa camelopardalis*), kudus (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), impalas (*Aepyceros melampus*), and elephants (*Loxodonta africana*). Browsing studies have been conducted in this ecosystem since the 1970s (Owen-Smith 1979, 1990, du Toit and Owen-Smith 1989, du Toit et al. 1990), and it appears that browsing-ungulate density and woody-vegetation cover have existed in an effectively stable equilibrium for decades, and presumably centuries, throughout the study area (du Toit 2003). Our experiments were carried out across heavily and lightly browsed *Acacia* stands at the top of the catenary drainage sequence. Sites were selected according to their distance from surface water, which is a powerful determinant of the distribution of herbivore biomass (see Naiman et al. 2003). Since the maximum distance between sites was <10 km, rainfall differences were considered negligible. More importantly, fire had not been recorded in the area for 13 years.

### *Tree description and browsing intensity*

Browsing effects were assessed on a deciduous palatable woody species, *Acacia nigrescens* Miller, which represents a staple food source for large mammalian browsers. The leaves are double pinnately compound and differ from those of many *Acacia* species in that they are not fine leaved, but have 4–6 leaflets, which are relatively large with oblique (lopsided) bases. Branches bear pairs of strong recurved thorns and prickles. Flowering mainly occurs from August to October (see Coates Palgrave et al. 2002). Leaf chemistry analyses of new leaves have shown relatively low concentrations of condensed tannin as well as total phenolics (du Toit 2003). After a preliminary vegetation survey, we identified six sites (25 ha each), each >1 km apart, at varying distances from either a seasonal or permanent waterhole. Three sites were heavily browsed, heavily grazed and trampled, and <1 km from water sources; three sites were less impacted by herbivores and >7 km from water. Evidence suggests that "available" soil nutrients in the forms of ammonium, nitrate, and water-soluble phosphorous are comparatively high at the


FIG. 1. Heavily browsed *A. nigrescens* tree canopies showing different shapes due to the impact of different ungulate browsers. Note the clear height of giraffe's browsing limit in the tree in panel (b). Photo credits: (a) D. A. Fornara; (b) J. T. du Toit.

waterholes (du Toit et al. 1990, Fornara 2005). We recorded ungulate browsing intensity on 30 trees randomly selected at each site (giving 90 trees $<1$ km and 90 trees $>7$ km from water). A total of 40 exposed shoots (i.e., terminal or leader shoots) were randomly selected all around each tree canopy within two height zones: 20 shoots at 0–2 m and 20 shoots at 2–4 m above ground level. Each shoot was examined for recent herbivory and scored as either browsed or unbrowsed. At the heavily browsed sites, 50–70% of exposed shoots were recently browsed in $>90\%$ of the surveyed trees. Trees had narrow canopies and were distinctively hedged by ungulate browsing (Fig. 1). All trees at the lightly browsed sites showed damage to only 10–20% of the exposed shoots, and were generally taller with wider canopies.

### *Clipping experiment: mass allocated to regrowth of shoots and leaves*

We used artificial clipping for comparing regrowth abilities between heavily and lightly browsed *Acacia* stands. The clipping experiment was set up with the following in mind: (1) decades of chronic ungulate browsing may have influenced whole tree size, as well as canopy size and shape (Fig. 1), and possibly affected root : shoot allocation patterns between heavily and lightly browsed plants (Bilbrough and Richards 1993); and (2) a high proportion of current-season shoots are pruned soon after sprouting at the heavily browsed sites (see our preliminary survey described in *Tree description and browsing intensity* and du Toit et al. 1990). Thus, it is difficult to measure true "compensatory growth" in such plants (see Bilbrough and Richards 1993) and/or to compare clipped and unclipped shoots within individual *Acacia* trees. Our aim, therefore, was to compare the regrowth abilities (e.g., total and net mass produced after clipping) of trees in monospecific stands exposed to low vs. high browsing intensity rather than to compare the regrowth responses of clipped and unclipped shoots within individual trees. Thus, we applied the same clipping regime to trees under high and low browsing intensity and used trees in lightly browsed sites as our reference sample. Within the constraints of vehicle accessibility, five trees per site (30 trees in total) were tagged with numbered aluminum tags. Across the open *Acacia* woodland those trees that were randomly selected for clipping within each site were $>50$ m apart. On each tree, 12 shoots (six shoots at 0–2 m and six shoots at 2–4 m above ground) were randomly chosen and clipping was performed at the end of February 2003. We clipped only shoots exposed to ungulate browsers at the edge of the canopy using, as a standard sampling unit, the giraffe browsing unit (GBU) to simulate mass loss due to browser damage (see grey circled area in Fig. 2a). The GBU is equivalent to the length of a shoot pruned or leaf-stripped by a giraffe in a single "bite" and, on average, corresponds to 14.4 cm of shoot measured directly into the canopy from the shoot's terminal end (Woolnough and du Toit 2001). The number of leaves per GBU was counted, and shoot diameter was measured with a caliper at the cut section. Then, an aluminum tag was secured on the remaining part of the shoot at 5 cm from the cut section. An unclipped shoot could remain between the cut section and the aluminum tag. For each of the 360 clipped GBU samples, composite shoot length was measured exactly using string, which allowed us to follow all shoot curvatures and all terminal shoots (ts) included in the GBU (Fig. 2a). Each clipped sample was then divided into its woody and leafy components (shoots and leaves), oven-dried for 3 d at 80°C, and weighed. Tagged shoots of the same trees were checked in June, September, and November for evidence of

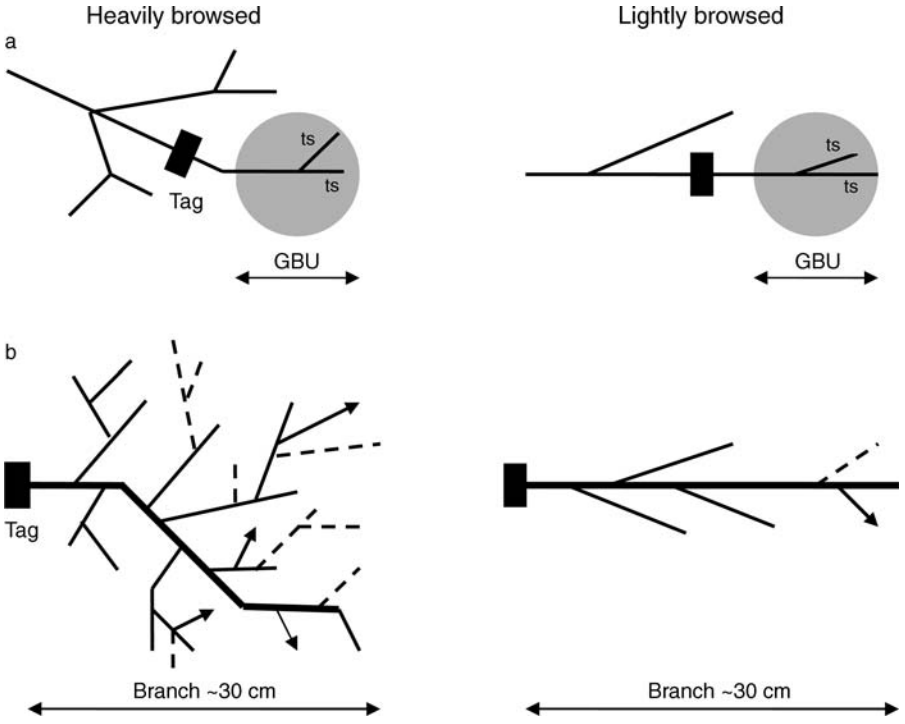


FIG. 2. Experimental diagrams for both (a) the clipping experiment and (b) the annual net branch growth measurements in *Acacia nigrescens* trees. (a) In the clipping experiment, the terminal shoots (ts) exposed to browsing were clipped in February 2003 using, as sample unit, the giraffe browsing unit (GBU) = 14.4 cm (ts included in the circled gray zone). Regrowth between the cut section and the tag was re-clipped in November 2003. Sample size = 360 GBUs. (b) In the annual net branch growth measurements, branches were tagged ~30 cm in from the canopy surface. All internodes (solid heavy lines) and side shoots (solid lines) were remeasured at 2, 9, 12, and 14 months, and any changes occurring between periods were reported on successive drawings. The dashed lines indicate apical shoot loss (browsed), whereas the arrowheads indicate increase in shoot length (regrowth) that would occur during the 14-month survey.

potential regrowth. New shoots sprouted during a 3–4 week window between October and November. They sprouted from lateral buds close to the previously cut section and were easily recognizable from their light-green color and the soft thorns. All new shoots grown between the tag and the cut section (including new regrowth on any unclipped shoot remaining between the cut section and the tag) were re-clipped in November, oven-dried for 3 d at 80°C, and weighed. The proportion of mass allocated to regrowth (net mass produced after clipping) was calculated as shoot mass of regrowth/shoot mass of GBU clipped. Any regrowth shoots that showed signs of browsing were excluded from the analysis. The percentage of browsed shoots in a random sample of 40 (20 shoots at 0–2 m and 20 shoots at 2–4 m height) was recorded at each site in June and November before the second clipping treatment.

In February 2003, 10 external branches per tree were randomly chosen and the length of the first three branch internodes was measured from the canopy surface inwards. On the same branches, the distances between the first five pairs of thorns were measured to determine thorn spacing. Additionally, thorn size was measured as the perpendicular distance from each thorn's hooked tip down to the junction of the thorn base with the branch. At the end of February, leaf samples (50 leaflets per tree) were collected from the same 30 trees to measure specific leaf area (SLA). Following Garnier et al. (2001), leaf collection was done early in the morning (05:00–07:00 hours) to minimize leaf dehydration and stored in moist paper in a cool box. Leaf area was measured within 24 h with a Model Area Meter (LI-COR, Lincoln, Nebraska, USA), and leaf samples were subsequently oven-dried for 2 d at 70°C.

### *Annual net branch growth under natural browsing intensity*

We performed a second set of experiments to quantify annual rates of branch growth for different *A. nigrescens* trees according to browsing intensity, tree height, and seasonality. Chronically browsed trees may show adaptive traits, such as increased annual branch growth rates, which would support the concept of browsing lawns. Effects of ungulate browsing were considered at two main height levels within tree canopies (0–2 m and 2–4 m) since giraffes are responsible for almost all browsing above 2 m (see du Toit 1990). This allowed us to address potential differences in shoot growth responses due to giraffe only vs. all browser species. We selected two sites within the study area: one <1 km from a seasonal waterhole, where

all *A. nigrescens* trees were heavily browsed; the other in a stand of lightly browsed *A. nigrescens* trees >7 km from the waterhole. We then randomly selected 10 trees within each site. On each tree, 10 branches (five at 0–2 m and five at 2–4 m) were marked with aluminum tags ~30 cm in from the canopy surface. The length of all internodes, side shoots, and terminal shoots (exposed to browsers) distal to each tag was measured as described in the previous section, and the position and distribution of all measured shoots and internodes was recorded in a "branch diagram" (see Fig. 2b). All tree branches were checked for signs of browsing, and each individual shoot/internode was remeasured after 2, 9, 12, and 14 months, respectively. At each measurement, each branch diagram was updated with any new shoot growth (arrowheads in Fig. 2b) or shoot loss due to ungulate pruning (dashed lines). Net branch extension (total branch growth minus browsed growth) was calculated after each inspection as the total difference between the length of all newly measured shoots and the length of all shoots recorded in the previous diagram.

To test for differences in tree branching between lightly and heavily browsed trees, a branching ratio was calculated in November 2003 using the same branches as were used for the annual branch growth experiment. The branching ratio sensu Archibald and Bond (2003) indicates whether branch growth is in the form of shoot elongation or lateral branching. For each branch unit, the ratio between the total length of all shoots and the length of the longest shoot was calculated and expressed as a mean of values collected after two growing seasons (in November 2002 and November 2003). The higher the ratio, the more numerous will be the side branches and, therefore, the tree branching.

Leaf samples were collected from each *Acacia* tree in November 2002 (early growing season), February 2003 (late growing season), and at the end of June 2003 (early dry season). Leaves were air dried and analyzed for N using the Kjeldahl standard method (Benton 1991). Finally, the numbers of flowers and pods were recorded in 2002 and 2003 around the whole canopy of 100 randomly selected trees across the three sites (33, 33, and 34 trees) per browsing intensity level (200 trees per year for two years).

### *Data analysis*

Samples obtained from each of the six sites were not assumed to be representative of the regions in which these sites occur (see Hurlbert 1984), but the study was designed to compare the response of monospecific stands of trees to high vs. low browsing intensity. We performed a general ANOVA using browsing as treatment and site as block to test for significant effects of herbivory on variation in mass of regrowth shoots and leaves after clipping. ANOVA was also used to test for changes in plant morpho-functional traits between heavily and lightly browsed sites as measured during the clipping experiment. Values were expressed as proportions when necessary and log-transformed to meet the assumptions of ANOVA. Correlation analysis was used to evaluate relationships between proportion of net mass produced in new leaves and shoots after nine months since artificial clipping ($y$), vs. browsing intensity ($x$) expressed as proportion of browsed shoots out of 40 shoots examined at random between ground level and 4 m in height and averaged across three seasonal measurements (February 2003, June 2003, and November 2003). ANOVA was also performed to test for the effects of browsing intensity, season, and canopy height (0–2 m and 2–4 m) on variation of annual net branch growth (values were log-transformed). A post hoc Tukey HSD test was then applied to evaluate interactive effects of different variables. A Friedman ANOVA and Kendall coefficient of concordance were used to test for significant variation in tree branching ratio between heavily and lightly browsed trees, also according to height in the canopy.

## Results

### *Clipping experiments: mass variation in regrowth of shoots and leaves*

Total mass compensated in leaves and shoots (Table 1) and proportion of mass allocated to regrowth (Fig. 3) nine months after clipping were both significantly higher in heavily browsed than lightly browsed *Acacia* stands. The highest percentage of tagged shoots browsed in November 2003 (just before the second clipping) on a single tree was ~20%. Heavily browsed stands of trees compensated with shoot regrowth equivalent to 12.9% ± 1.2% (all data reported as mean ± SE) of initial shoot mass, and leaf regrowth equivalent to 62.8% ± 8.7% of initial leaf mass (Fig. 3). Lightly browsed stands of trees compensated with shoot regrowth equivalent to 5.46% ± 0.65% of initial shoot mass and 27% ± 3.42% of initial leaf mass (Fig. 3). Mean values of all other measured morpho-functional traits, except thorn size, leaf density, and leaf : shoot ratio, were all significantly affected by ungulate browsing (Table 1). The higher number of shoots produced by heavily browsed trees suggests that the removal of apical dominance stimulated the growth of secondary shoot meristems. There was a positive correlation between the proportion of biomass produced in both regrowth shoots and leaves after clipping and the proportion of browsed shoots averaged across three seasonal measurements (Fig. 4). Mean values of SLA measured in the mid to late growing season were similar in heavily (94.1 ± 2.5 $cm^2$/g) and lightly (92.4 ± 2.5 $cm^2$/g) browsed sites, resulting in no significant variation in SLA across browsing intensities ($F_{1,4} = 1.76$, not significant).

### *Annual net branch growth, leaf N, and phenology*

Overall, our results show that *A. nigrescens* trees, regardless of browsing intensity, concentrated their main annual growth between September and November (Fig. 5). In four weeks, net branch length (calculated from

TABLE 1. Mean values (±SE) and ANOVA statistics for variation of *Acacia nigrescens* morpho-functional traits measured as part of the clipping experiment.

| Trait | Browsing intensity | | Browsing effect | | |
|---|---|---|---|---|---|
| | High | Low | df | *F* | *P* |
| Shoot mass (g) | 0.12 ± 0.02 | 0.03 ± 0.07 | 1, 4 | 21.4 | 0.01 |
| Leaf mass (g) | 0.39 ± 0.05 | 0.17 ± 0.04 | 1, 4 | 40.5 | 0.003 |
| Shoot length (mm) | 202 ± 26.8 | 60.1 ± 8.9 | 1, 4 | 106.7 | <0.001 |
| Number of leaves | 14.5 ± 1.94 | 4.85 ± 0.45 | 1, 4 | 30.6 | 0.005 |
| Leaf density (leaves/cm) | 0.074 ± 0.01 | 0.078 ± 0.02 | 1, 4 | 0.56 | NS |
| Leaf : shoot ratio | 5.67 ± 0.49 | 6.15 ± 0.68 | 1, 4 | 0.41 | NS |
| Number of shoots | 2.34 ± 0.15 | 1.12 ± 0.09 | 1, 4 | 22.4 | 0.01 |
| Shoot diameter (mm) | 3.37 ± 0.15 | 2.75 ± 0.11 | 1, 4 | 14.2 | 0.02 |
| Internode length (mm) | 58.5 ± 3.37 | 107 ± 14.1 | 1, 4 | 8.70 | 0.04 |
| Thorn size (mm) | 4.33 ± 0.19 | 3.97 ± 0.16 | 1, 4 | 0.77 | NS |
| Thorn spacing (mm) | 19.3 ± 0.80 | 26.5 ± 1.45 | 1, 4 | 14.7 | 0.02 |

*Notes:* Total mass of shoots and leaves, shoot length, number of shoots and leaves, leaf density, and leaf : shoot ratio were measured on regrowth nine months after clipping. All listed traits were compared across heavily and lightly browsed sites (three sites per browsing level). Standard errors represent variation among sites within the high and low browsed intensity categories. NS = not significant.

data collected in two consecutive years), increased by 36.5% ± 2.78% in heavily browsed stands and by 18% ± 0.97% in lightly browsed *Acacia* stands (Fig. 5). Seasonal effects of mean branch length were significant (Fig. 5), and the Tukey HSD test showed that such differences were mainly due to shoot sprouting between September–November 2002 and September–November 2003. Moreover, annual net branch growth was significantly affected by browsing intensity and tree height as well as by a browsing × season interaction (Fig. 5). Mean net branch growth was higher in heavily browsed sites (398 ± 63 mm in November 2002 and 434 ± 52 mm in November 2003) than lightly browsed sites (195 ± 43 mm in November 2002 and 125 ± 19 mm in November 2003). However, there was no interaction between browsing, seasonality, and height (Fig. 5). The mean number of new shoots produced after 14 months (including two growing seasons) within branches of *Acacia* trees was 9.3 ± 0.68 shoots in heavily browsed stands and 3.44 ± 0.37 shoots in lightly browsed stands ($F_{1, 144} = 48.4$, $P < 0.001$). Branching ratio was positively correlated with browsing intensity ($F_{1, 144} = 23.8$, $P < 0.001$; Fig. 6), and heavily browsed sites showed greater branching than lightly browsed sites.

Variation in leaf N concentration was related to season (Fig. 7), so that, regardless of browsing intensity, leaf N content was highest during the main growing season (November), and decreased in the late growing season (February) to be lowest in the early dry season (June; $F_{2,18} = 180.2$, $P < 0.0001$; Fig. 7). Nevertheless, browsing intensity was associated with significant variation in leaf N content ($F_{1,18} = 12.8$, $P < 0.0001$) and interacted with season ($F_{2,18} = 111.1$, $P < 0.0001$); our data show high leaf N levels in heavily browsed trees during the main growing season (November 2002; Fig.

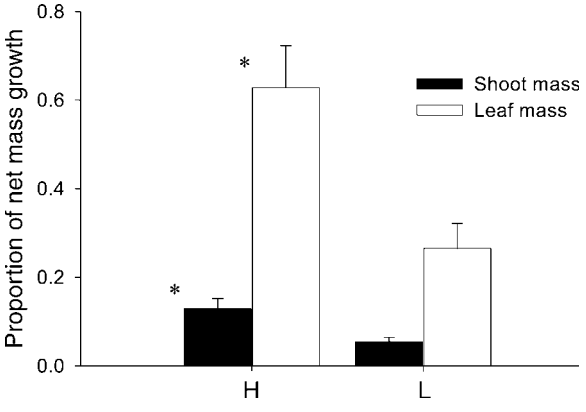


FIG. 3. Proportion of mass growth in shoots and leaves of heavily browsed (H) and lightly browsed (L) *A. nigrescens* trees nine months after clipping. Standard errors show variation among sites within the H and L categories. Asterisks indicate $P < 0.05$.

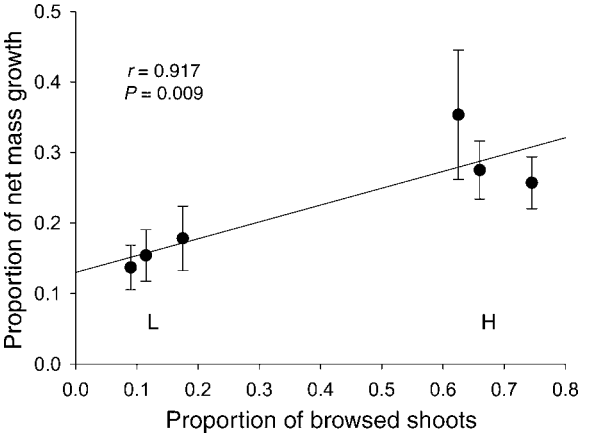


FIG. 4. Relationship between the proportion of browsed shoots (averaged from February 2003, June 2003, and November 2003 measurements) and the proportion of total mass produced since clipping at heavily browsed (H) and lightly browsed (L) sites. Net mass in regrowth was calculated as (mass in regrowth)/(mass of GBU clipped). Error bars show ±SE and represent variation among sites within the high and low browsed intensity categories.

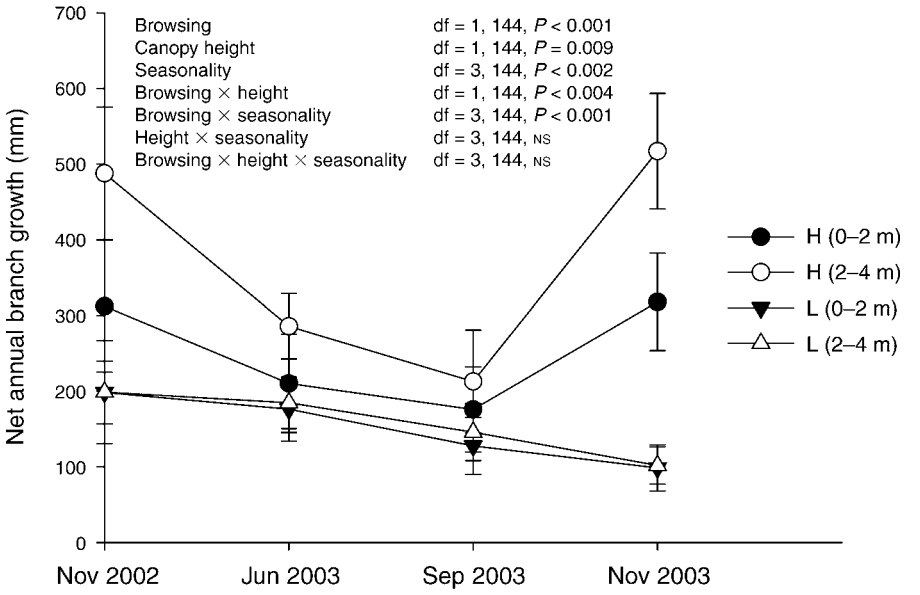


FIG. 5. ANOVA results and annual net branch growth (cm) of heavily (H) and lightly (L) browsed *A. nigrescens* stands. Branch extension was measured at two different canopy height levels (0–2 m and 2–4 m) at five time intervals. Error bars show ±SE and represent length variation among H and L sites.

7). Moreover, heavily browsed *A. nigrescens* trees appear to have withdrawn N from their leaves more efficiently than lightly browsed trees at the end of the growing season (June 2003; Fig. 7).

Browsing pressure on *A. nigrescens* trees was found to influence the allocation of resources to reproductive plant parts. The percentage of flowering trees was 36% in lightly browsed sites and 25% in heavily browsed stands, while the number of flowers per tree was extremely variable. Browsing pressure had no significant effect on the number of flowers produced by trees exposed to high or low browsing intensity ($F_{1,4} = 0.93$, not significant) but 35% of trees carried pods in lightly browsed sites compared to only 16% in heavily browsed sites. Moreover, the mean number of pods per tree differed significantly between lightly (75 ± 5.6 pods) and heavily (10 ± 2.4 pods) browsed *Acacia* stands ($F_{1,4} = 92.4$, $P < 0.001$).

## DISCUSSION

Our findings demonstrate that "browsing lawns" occur in African savannas in a manner analogous to

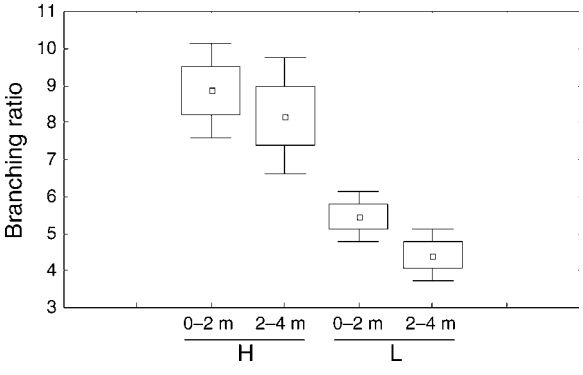


FIG. 6. Variation in branching ratio between H and L sites (and canopy heights) measured as part of the net branch growth experiment. Standard errors represent variation within tree height among H and L sites. The branching ratio indicates whether branch growth is in the form of shoot elongation or lateral branching and is calculated as the total length of all branch shoots divided by the length of the longest shoot. The small squares are mean values, boxes indicate mean ± SE, and error bars show ±1.96 SE.

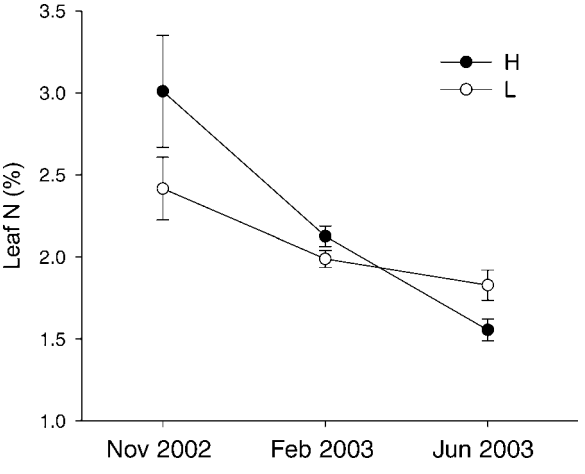


FIG. 7. Variation in leaf N (%) between heavily (H) and lightly (L) browsed *Acacia* stands (20 trees) according to season. Bars represent mean ± 1.96 SE. Standard errors represent variation among sites within the high and low browsed categories.

that of grazing lawns (McNaughton 1983, 1984), whereby large herbivores induce changes in resource allocation and plant architecture that increase the regrowth of foliage in heavily browsed *Acacia nigrescens* stands. We found evidence that *A. nigrescens* trees are able to resprout and survive under a chronic browsing regime, where heavily browsed trees rely on the facultative adjustment of eco-physiological mechanisms to sustain regrowth, which is consistent with the results of previous studies in African savannas (Pellew 1983, du Toit et al. 1990, Dangerfield and Modukanele 1996, Gadd et al. 2001) and in temperate and boreal forests (Bergström and Danell 1987, Edenius et al. 1993, Peinetti et al. 2001). However, the analogy with grazing lawns is not complete because, while ungulate grazing indirectly increases the grass leaf : stem ratio, this is not the case with browsing lawns, since we found the leaf : shoot ratio in regrowth shoots to be similar across heavily and lightly browsed *Acacia* stands. This was due to rapid shoot extension in heavily browsed trees after clipping, which is required to support increased leaf growth. Our evidence is that browsing lawns increase the feeding efficiency of browsers through increased production of shoot mass all around the distinctively hedged canopies of browsed trees. This makes more food available to ungulate browsers such as giraffes, kudus, and impalas, which often remove shoot ends and, hence, have a pruning effect (Pellew 1983, du Toit et al. 1990). Leaf mass did also increase in regrowth shoots, which enhances the value of each bite for a browsing ungulate. Moreover, leaves of browsed trees appear to be highly palatable (i.e., high N:C ratio) because of reduced intershoot competition, which improves the nutrient : condensed tannin ratio and maintains the browsing–regrowth feedback loop (du Toit el al. 1990). The strong relationship between leaf nitrogen, SLA, and photosynthetic capacity (see Reich et al. 1995, 1999) suggests that the higher leaf N content in heavily browsed trees in the early growing season supported higher photosynthetic rates that, in turn, promoted higher growth rates. Finally, the main period of plant growth for both heavily and lightly browsed *Acacia nigrescens* plants occurred just before the onset of the wet season. This pulsed growth is dependent on the availability of nutrient reserves within the tree, some of which are stored from the previous growing season (Scogings et al. 2004). We found evidence to suggest that individual trees adapt to browsing by adjusting the re-allocation of N from leaves to perennial organs; heavily browsed trees withdrew more N than lightly browsed trees in June, at the beginning of the dry season (Fig. 7). This, combined with a reduced canopy volume and reduced intershoot competition, might explain the comparatively enhanced ability of heavily browsed plants to resprout after the clipping treatment. However, we did not measure net or total aboveground growth per entire plant (or per stand), as has been done for grazed systems (McNaugthon 1984, Hik and Jefferies 1990), and so, whether total aboveground productivity is higher in lightly vs. heavily browsed *Acacia* stands remains to be answered.

Our study did reveal the coexistence of tolerance and resistance traits in heavily browsed trees. Physical defenses limit the feeding efficiency of browsers (Cooper and Owen-Smith 1986), and so, thorns represent a relatively "cheap" form of plant protection, especially if amortized over many years on the relatively N-rich soils (Craine et al. 2003) of semiarid eutrophic African savannas (Scholes et al. 2003, Venter et al. 2003). Thorns, prickles, or spines provide at least partial protection to critical photosynthetic tissues that allow the plant to recover from browsing (Cooper et al. 2003), which is when shoots are undergoing rapid regrowth. Heavily browsed woody plants can maintain their dominance within the plant community due to their tolerance traits (Augustine and McNaughton 1998), and this seems to be the case for *A. nigrescens*, which exhibits traits for both tolerance (rapid regrowth) and resistance (spinescence). This implies that a trade-off between tolerance and resistance may not occur in natural *Acacia* stands under chronic ungulate browsing, and hence, the evolution of different plant defensive strategies may not be constrained (Leimu and Koricheva 2006). Although ungulate browsers maintain densely hedged tree canopies in a plant–herbivore interaction that is in some ways analogous to that which maintains grazing lawns (McNaughton 1983, 1984), the overall effects on nutrient cycling, either within the plant–browser system or at the ecosystem level, are probably different. The browsing system involves sedentary ungulates that forage alone or in small groups, while grazing ungulates typically occur in herds that continually move across the landscape, sometimes in large migrations. This means that while regrowth within grazing lawns is cropped in an intermittent pattern of periodically intense herbivory (Augustine and McNaughton 1998), chronically hedged *Acacia* stands are continually exposed to browsing throughout the growing season. Further research is needed to understand the nutrient dynamics involved; i.e., the nutrient source–sink systems that support plant regrowth abilities, such as nutrient remobilization, high levels of $N_2$ fixation in fine-leaved savannas (Scholes et al. 2003), root mining triggered by aboveground herbivory (Bardgett and Wardle 2003), the effects of ungulate dung and urine on soil nutrient dynamics at heavily browsed and grazed sites, and, finally, the potential effects of large herbivores on fine-root growth of woody plants (Ruess et al. 1998). In these semiarid systems there is also the (as yet unexplored) possibility that palatable trees can persist even in areas of high ungulate density due to a trade-off between the risks of browsing and drought, whereby the reduced canopy of a heavily browsed tree improves water balance and

competition with grasses for water is reduced by locally intense grazing.

Finally, a particularly significant issue when comparing grazing and browsing "lawns," is to consider whether heavily browsed trees can maintain the reproductive success required for a stand of browsed trees to persist in the long term. We found fewer trees carrying pods and fewer pods per tree in heavily browsed sites, suggesting a long-term negative effect of chronic browsing on plant reproductive success. It is likely that only the few individuals that escape browsing during favorable years could produce a viable pod crop within heavily browsed stands of *A. nigrescens,* and those trees would have reached a "size refuge" such that their canopies are mainly above the reach of giraffes, the tallest browsers. We thus hypothesize that the persistence of browsing lawns has less to do with browsing pressure on stunted and hedged trees within the browsing zone and more to do with the survival of a few large individual trees that supply propagules within a source–sink system. Such trees are vulnerable to felling and bark-stripping by elephants, exemplifying the complexity of interactions that underlie the spatiotemporal heterogeneity of African savannas (Naiman et al. 2003).

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## DATA REGISTRY

Data associated with this paper are registered (ESA Data Registry: 31.1).